J. Math. Biol. (1999) 38: 534–570

Journal of
Mathematical
Biology

A non-local model for a swarm

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Received: 17 September 1997 / Revised version: 17 March 1998

Abstract. This paper describes continuum models for swarming behavior based on non-local interactions. The interactions are assumed to influence the velocity of the organisms. The model consists of integro-differential advection-diffusion equations, with convolution terms that describe long range attraction and repulsion. We find that if density dependence in the repulsion term is of a higher order than in the attraction term, then the swarm profile is realistic: i.e. the swarm has a constant interior density, with sharp edges, as observed in biological examples. This is our main result. Linear stability analysis, singular perturbation theory, and numerical experiments reveal that weak, density-independent diffusion leads to disintegration of the swarm, but only on an exponentially large time scale. When density dependence is put into the diffusion term, we find that true, locally stable traveling band solutions occur. We further explore the effects of local and non-local density dependent drift and unequal ranges of attraction and repulsion. We compare our results with results of some local models, and find that such models cannot account for cohesive, finite swarms with realistic density profiles.

Key words: Swarming behavior – Aggregation – Non-local interactions – Integro-differential equations – Traveling band solutions

1. Introduction

Partial differential equations with diffusive terms are traditionally used to describe spatially distributed populations (Skellam, 1951; Fisher, 1937; Okubo, 1980; Murray, 1989). However, while many of the traditional models can describe phenomena such as invasions, represented by **traveling wave solutions** (Fisher, 1937; Dunbar, 1983; Conley and Fife, 1982; van den Bosch et al., 1988; Ludwig et al., 1979), none can give rise to realistic representations of a finite group of individuals migrating together (e.g. a swarm or flock). This phenomenon must be described mathematically by a **traveling band solution** since the density tends to zero both in front of, and behind the swarm. The difficulties of constructing *biologically meaningful* partial differential equation (PDE) models with this behavior were described lucidly in a pedagogical exposition by Odell (1980). A recent paper describes several attempts to model locust swarm migration (Edelstein-Keshet et al., 1997) based on biologically reasonable hypotheses. The conclusions are mostly negative, pointing to the difficulties of describing a cohesive, compact swarm with traditional models. However, recognition of this fact is underrepresented in classical texts (Murray, 1989; Okubo, 1980; Conley and Fife, 1982). Further, recent work which claims to describe properties of herd migration (Gueron and Liron, 1989) is based on assumptions which are difficult to justify biologically. Several surveys give an overview of the models for aggregations (Grunbaum and Okubo, 1994; Parrish and Hammer, 1997; Okubo, 1986; Okubo, 1980; Turchin, 1997).

Though PDE models are popular due to a rich mathematical experience (Holmes et al., 1994), they are at best an approximation. A recent interest in models that include non-local effects has led to the investigation of **integro-differential equation** models. These can describe interactions at a distance, e.g. due to vision, hearing, and other senses. Some examples of such models have appeared in the literature (Kawasaki, 1978; Cohen and Murray, 1981; Levin and Segel, 1985; Murray, 1989; Mogilner and Edelstein-Keshet, 1996; Lui, 1983; Creegan and Lui, 1984; Mimura and Yamaguti, 1982; Nagai and Ikeda, 1991; Turchin, 1986; Edelstein-Keshet et al., 1997). See also Grunbaum and Okubo (1994) and Flierl et al. (1998) for reviews. There are several recent examples of models with nonlocal effects in the speed of motion of organisms (Grindrod, 1998; Mogilner and Gueron, 1998; Edelstein-Keshet et al., 1997). Numerous recent publications include nonlocal effects in the production terms, e.g. birth of new individuals at a distance from the parent organisms, as in the case of seed dispersal (Kot et al., 1996; Lewis, 1997, Allen et al., 1996, Lefever and Lejeune, 1997; Boldrini et al., 1997).

In this paper, we consider an integro-differential equation model that is simple enough to be treated analytically. The model captures the idea of attraction-repulsion interactions between organisms. We show that the notion of a globally stable *true traveling band solution* is still abstract, rather than biologically realistic, but that *nearly band-like solutions* can be found in such models. We investigate the effects of various terms in such a model, and show how certain terms, acting together, can improve the cohesion of traveling bands, though none can actually prevent the loss of straying individuals. We show that if the random motility of the organisms vanishes at very low swarm density, then *locally stable* traveling band solutions can exist.

The philosophy of the model here follows that of Novick and Segel (1984) where requirements for strict traveling bands were replaced by weaker conditions that led to quasi-traveling band solutions, i.e. solutions that change shape very gradually. They showed that their chemotactic system was characterized by two distinct time scales, a fast and a slow one. Motion occurs on the fast time scale, while changes in shape occur on the slow time scale. This accounts for the motion of the swarm, without the need for unrealistic assumptions.

2. Background summary of integro-differential population models

In the traditional population models (Murray, 1989; Okubo, 1980; Holmes et al., 1994), a single-species, spatially distributed population is described by an equation of the form:

$$\frac{\partial f}{\partial t}=\frac{\partial}{\partial x}\left(D(f)\,\frac{\partial f}{\partial x}\right)-\frac{\partial}{\partial x}(V(f)f)+B(f). \tag{1}$$

This **diffusion-advection-reaction** equation governs the spatio-temporal dynamics of the population density $f(x, t)$, where the spatial variable, x, is, in this case, one-dimensional.

The first term on the right hand side of Eq. (1) describes random motion. $D(f)$ is the corresponding diffusion coefficient. The second term is advection with velocity $V(f)$, and the third term is growth (or decay) of the population with rate $B(f)$. These rates of diffusion, advection and growth may be density dependent. A derivation of the detailed diffusion and advection terms based on individual behavior (such as jumps and turns) is described in a number of papers (Alt, 1980; Othmer et al., 1988; Grunbaum, 1984). We will not consider these precise biological details here, since our aim is to understand how non-local terms operate together. This problem is challenging mathematically, and it is premature to formulate it with the detailed biology in place.

In **Fisher's equation** (Fisher, 1973; Murray, 1989; Conley and Fife, 1982), and related models it is the logistic population birth terms, $B(f) = f(1 - f)$, that essentially prescribe the traveling wave behavior of the solution. However, in models which describe motion on a short time scale (that is, short with respect to the generation time of the organism) the terms for birth and death can be neglected, i.e. $B(f) = 0$. In this paper, we will not consider growth terms, and focus exclusively on non-linear and non-local transport properties of the population.

Density dependence in the diffusion coefficient (Bertsch et al., 1985; Bertsch et al., 1984) means that the random motility changes in response to the density. For example, it is known that the random tumbling of certain types of bacterial cells (Odell, 1980; Sherratt, 1994) is density dependent. Density dependence in the advection term means that the velocity of the organism is adjusted to the local population density. This is observed in myxobacterial swarms where the swarming rates are increasing functions of the density of the swarm (Kaiser and Crosby, 1983). In general, the advection velocity and diffusion coefficient may also depend on local density gradients. Biologically, such factors lead to local aggregation (attraction) or dispersal (repulsion) of the organisms.

Though there are many speculations and experimental observations, it appears that a quantitative framework for understanding swarming behavior is still lacking. In the recent review, Parrish (1997) summarizes the situation: "Order is seen, but it is not immediately obvious how to quantify it". Experimental work is challenging, and models can provide a tool for solving the inverse problem, namely, of identifying which of various possible sets of individual interactions might be consistent with the observed patterns of population behavior. For example, one common observation is that the density of the interior of a swarm is relatively constant and uniform, independent of the total swarm size. Another observation is that the edges are abrupt. Models with diffusion as the only dispersive effect cannot explain such observations because the density in the core of a swarm is predicted to grow with the number of organisms. Models with active repulsion between organisms can correct this defect, as we will show.

Several biological papers describe properties of fish schools (Keenleyside, 1995; Breder, 1954; Ranta et al., 1992) and bird flocks (Miller and Stephen, 1966; Conder, 1949; Emlen, 1952). For example, Keenleyside (1995) measured the deviation of groups of sticklebacks and rudd from a uniform distribution and noted that larger groups of fish attract a single individual more strongly than smaller groups (Keenleyside, 1995; Krause and Tegeder 1994; Tegeder and Krause 1995; Breder, 1954; Nakamura, 1952). The idea that individuals seek some uniform density – or distribute themselves with a nearly constant *individual distance* between them is a common observation (Conder, 1949; Emlen, 1952; Miller and Stephen, 1966). For example, gulls space themselves roughly one body length apart (Emlen, 1952) whereas tufted ducks prefer 2-3 body lengths spacing (Conder, 1949). Sandhill cranes maintain an individual distance of about 5.8 ft, regardless of flock size (Miller and Stephen, 1966). Many of the biological papers recognize that the spacing or density of the group stems from opposing forces of attraction and repulsion (Emlen, 1952; Breder, 1954; Miller and Stephen, 1966) and some further emphasize that these forces vary with distance between the organisms and stem from distinct sensory mechanisms (Breder, 1954; Krause and Tegeder 1994; Tegeder and Krause 1995). Short range repulsion to avoid overcrowding and collisions and long range attraction to keep the group together are discussed by Breder (1954). Some theoretical work on the types of attraction and repulsion functions and the implications of behavior-distance relationships to spatial patterns is given by Warburton and Lazarus (1991) using individual-based simulations.

In this paper, we investigate a type of non-local advection, leaving the dispersal term in a more traditional local form. Convection terms lead to attraction, repulsion, and macroscopic motion. When we use a non-local description of the advection of organisms, we are allowing the speed and direction of motion of an individual to be determined by some average of the density in its environment. The average may give more weight to information about individuals that are closer, or those that are farther away. For example, individuals may avoid direct contact, i.e. exclude one another from some zone of repulsion, but be attracted to one another in some larger annulus (Okubo, 1980; Mogilner and Gueron, 1998). Because biological sensory systems have some limitations, it is natural to assume that the interactions have some finite spatial extent or drop off rapidly with distance beyond some range. Typically, terms in the advective velocity have the form of a convolution (Mogilner and Edelstein-Keshet, 1996), i.e.,

$$V(f) = K * f = \int_R K(x - x')f(x', t)\,dx'. \tag{2}$$

This form describes the velocity induced at the site x by the net effects of all individuals at various sites x'. The **kernel** $K(x - x')$ associates a strength of interaction per unit density with the distance $x - x'$ between any two sites. The interactions take place over some finite domain, R. This is a "minimal" non-local form which assumes pair-wise interactions and linear superposition of influences in the population. This simple form already leads to some qualitatively new patterns of motion, as we will show.

Many biologically based models have already examined the interaction of a species with a natural food or nutrient distribution (Keller and Odell, 1975; Odell and Keller, 1976; Keller and Segel, 1971; Odell, 1980; Novick-Cohen and Segel, 1984; Nagai and Ikeda, 1991; Gueron and Liron, 1989) but this is not the main thrust of our paper. Thus, we consider only one species and deemphasize consumption of resources.

3. Description of the model

Below, we discuss a particular form of the one dimensional advection-diffusion equation that has been used to model swarming behavior (Edelstein-Keshet et al., 1997; Kawasaki, 1978; Grunbaum and Okubo, 1994; Mimyura and Yamaguti, 1982; Nagai and Ikeda, 1991; Grindrod, 1998):

$$\frac{\partial f}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial f}{\partial x} - Vf\right). \tag{3}$$

Here x is a one-dimensional coordinate, t is time, $f(x, t)$ is the swarm density. For simplicity, we assume that diffusion is density independent, with corresponding constant coefficient D (the consequences of the density dependent diffusion will be discussed in Sect. 6.4). The second term describes the drift of organisms with a non-local, density-dependent velocity V.

Analytically, the existence of solutions to certain non-local versions of this equation was demonstrated (Grindrod, 1988) and stability analysis of the homogeneous steady state to small perturbations have been investigated (Kawasaki, 1978; Grindrod, 1988). Singular perturbation analysis in the limit of weak diffusion demonstrated the existence of sharp peaks in the distribution of the population density (Mogilner et al., 1996). Numerical simulations of similar equations have been carried out in Turchin (1986) and in Edelstein-Keshet et al. (1997).

In our own investigation, the group velocity term is determined at a given position by a weighted interaction with the neighbors. Though we will consider the combined effects of several non-local terms, we first discuss special cases. It is helpful, when considering the effects of these terms, to visualize a particularly simple swarm shape, consisting of a rectangular band: i.e. a total number N of individuals distributed evenly over an interval of length L. We can then describe how various advection terms affect the velocities inside the swarm and at its edges.

3.1. Drift with a strictly even kernel

Consider the situation that

$$V(f) = A_e K_e * f = A_e \int_{x-r}^{x+r} K_e(x - x') f(x', t)\, dx', \tag{4}$$

where A_e is a positive constant. We assume that the kernel has compact support, and that r is the "sensing radius" of the organisms. We further assume that K_e is a positive, even function ($K_e(x) = K_e(-x)$) on the interval $[-r, r]$ and zero otherwise, which implies that the organisms react identically to density in front and behind.

If the rectangular swarm is large enough that an individual inside is not aware of the swarm edges (i.e. $L > 2r$), then inside the swarm, (where $f = F =$ constant), the velocity would be

$$\begin{aligned} V(f)_{inside} &= A_e \int_{x-r}^{x+r} K_e(x - x') f(x', t)\, dx' \\ &= A_e F \int_{-r}^{r} K_e(-x')\, dx' = A_e F. \end{aligned}$$

This follows from normalization of the kernel which ensures that

$$\int_{-r}^{r} K_e(x')\, dx' = 1.$$

If the individual is at the front edge of a rectangular pulse swarm (assumed to be at $x = L$ where L is the width of the swarm), then its velocity would be

$$\begin{aligned} V(f)_{frontedge} &= A_e \int_{L-r}^{L+r} K_e(L - x') f(x', t)\, dx' \\ &= A_e F \int_{-r}^{0} K_e(-x')\, dx' = \tfrac{1}{2} A_e F. \end{aligned}$$

Thus, the drift velocity is slow if there are no others in front. It is easily shown that the same result occurs at the back edge of a rectangular band, i.e.

$$V(f)_{backedge} = \tfrac{1}{2} A_e F.$$

We can conclude that **a non-local velocity with an even kernel gives rise to a group drift** (see Fig. 1). This implies that some type of environmental cues are present so that there is a directionality inherent in the coordinate system. The speed of the drift is proportional to the density averaged over distance. Where an organism is completely surrounded by others, this term has greatest effect. Edges of the swarm

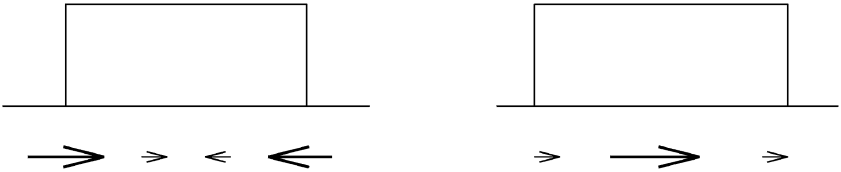


Fig. 1. The effects of an odd kernel (left) and an even kernel (right) on velocities induced on individuals inside a swarm. The density of the swarm in space is shown here as a simple rectangular band. Note that the odd kernel causes organisms at the front and rear edge to move back towards the center of the swarm. The odd kernel has very little effect inside the swarm where the density is constant. By comparison, the even kernel induces a collective motion of the swarm as a whole. (This implies some external environmental cues.) The effect of the even kernel is greatest inside the swarm.

are associated with lower drift speeds. We will demonstrate that this averaging of the non-local drift has an important effect on the stability of the swarm. Indeed, in the local case, the speed of individuals behind the rear edge of the swarm drops sharply to zero. This causes the swarm to disintegrate, losing individuals from its rear. The non-local drift leads to a slower and smoother change in the velocity of individuals close to the swarm. This slows down the disintegration, though it does not eliminate it completely.

3.2. The effect of an odd kernel

We now consider the situation in which

$$V(f) = A_o K_o * f,$$

where K_o is an odd function on the interval $[-r, r]$, and is zero outside this interval, and A_o is a constant. We will assume that $K_o(x) \leqq 0$ at $x > 0$ and that the following normalization property holds:

$$\int_{-r}^{0} K_o(x')\,dx' = \tfrac{1}{2}.$$

Then, for an individual inside the swarm:

$$\begin{aligned} V(f)_{inside} &= A_o \int_{x-r}^{x+r} K_o(x-x')\,f(x',t)\,dx' \\ &= A_o F \int_{-r}^{r} K_o(-x')\,dx' = 0. \end{aligned}$$

This implies that in regions in which the density is uniform (for swarms larger than r), an odd kernel has no effect.

By repeating this calculation at the front and at the back edge of a rectangular swarm, we find that

$$V(f)_{frontedge} = A_o F \int_{L-r}^{L} K_o(L - x')\, dx' = -\tfrac{1}{2} A_o F,$$

$$V(f)_{backedge} = \tfrac{1}{2} A_o F.$$

This shows that **an odd kernel has an effect where there are uneven distributions of density, for example at the edges of the swarm** (see Fig. 1). It is also apparent that sign of the velocity changes if the higher density is in front or in back of a given individual. Thus, odd kernels can describe the tendency to turn back at the front edge, or to move faster and catch up at the back edge.

Odd kernels can be used to describe both attractive and repulsive influences. We assume that $K_o(x) \leqq 0$ at $x > 0$. Then $A_o > 0$ corresponds to attraction (convergence of the organisms to regions of higher density), and $A_o < 0$ describes repulsion (divergence from aggregation sites).

3.3. The model with a combination of drift terms

We now look at a composite model with a combination of terms, and discuss what happens to the density distribution under various scenarios. We take, for the model, equation (3) together with the velocity,

$$V(f) = a_e f + (A_a - A_r f)(K_o * f). \tag{5}$$

In equation (5), the coefficients represent attraction ($A_a > 0$), repulsion ($A_r > 0$), and local (a_e) terms in the density-dependent motion. The aggregation kernel K_o is an odd function with compact support, whose detailed structure will be explained below. Note that the dimensions of the parameters are: $[a_e]$, $[A_a]$ = velocity/density, $[A_r]$ = velocity/density^2. If the local density is $F = A_a/A_r$ then attraction and repulsion exactly balance and the non-local terms vanish in this expression.

The character of the non-linearity in the model deserves special attention. Diffusion is taken to be density independent (but see later remarks). The even drift term and the attraction term are proportional to density. This means that beyond some critical density, aggregation would dominate over dispersal, and there would be unidirectional motion of the group. We use a simple local drift term for the analysis, and investigate a non-local term in numerical studies (Sect 8.2). Repulsion is more non-linear, i.e. proportional to a product of a non-local factor and the local density. This means that when the local density is low, there is almost no repulsion, and when it is high, the repulsion is much greater than the attraction. These non-linearities lead to cohesion of the swarm. Further, they prevent blow-up or degeneracy such as collapse of the swarm into an unrealistic highly localized and dense group, when there are many individuals present (Edelstein-Keshet et al., 1997; Mogilner et al. 1996).

The specific form of the repulsion term allows for tractability of analysis of this model. One might in general expect some non-linear convolution terms in realistic models, but their analysis is prohibitively complicated. We believe that the results with this simplified version are generic in some sense, and we are currently exploring several generalizations in the context of individual based models.

4. Onset of aggregation

In this section, we explore the onset of aggregation in the swarm. We consider the case in which the attraction and repulsion have different spatial ranges that is biologically realistic:

$$V(f) = a_e f + A_a(K_a * f) - A_r f(K_r * f), \tag{6}$$

where

$$K_a(x) = -\frac{x}{2a^2}\exp(-x^2/2a^2), \qquad K_r(x) = -\frac{x}{2r^2}\exp(-x^2/2r^2), \tag{7}$$

are, respectively, the normalized attraction and repulsion kernels. Biological evidence suggests that for interactions between swarm members, repulsion has a shorter range than the attraction, so that $r < a$.

Consider the stability of a homogeneous distribution of organisms, F, to a small perturbation of the form

$$f(x, t) = F + e(x, t),$$

such that $|e(x, t)| \ll F$. Plugging this form into the equations of the model (equations (6) and (3)) and keeping only terms linear in e, we find the following equation:

$$\frac{\partial e}{\partial t} = D\frac{\partial^2 e}{\partial x^2} - \frac{\partial}{\partial x}(2a_e Fe + A_a[F(K_a * e) + e(K_a * F)]$$
$$- A_r[F^2(K_r * e) + 2Fe(K_r * F)]).$$

Because both kernels are odd and F is constant, terms containing convolutions $(K_{a,r} * F)$ cancel, and we have:

$$\frac{\partial e}{\partial t} = D\frac{\partial^2 e}{\partial x^2} - \frac{\partial}{\partial x}\left(2a_e F e + A_a F(K_a * e) - A_r F^2 (K_r * e)\right). \tag{8}$$

We look for perturbations of the form $e(x, t) \sim \exp(\lambda t)\exp(iqx)$. Plugging this perturbation into (8) we obtain the linear growth rate $\lambda(q)$ associated with the wavenumber q:

$$\lambda(q) = -Dq^2 - 2iqa_e F - iqA_a F\hat{K}_a(q) + iqA_r F^2 \hat{K}_r(q), \tag{9}$$

where $\hat{K}_a(q)$ and $\hat{K}_r(q)$ are the Fourier transforms of the kernels, which are:

$$\hat{K}_a(q) = iqa\exp(-q^2a^2/2), \qquad \hat{K}_r(q) = iqr\exp(-q^2r^2/2). \tag{10}$$

Substituting these forms into the growth rate (9), we find that the real part of the growth rate (which is responsible for the growth rate of the perturbations) is:

$$\mathrm{Re}(\lambda(q)) = q^2(F[A_a a\exp(-q^2a^2/2) - A_r rF\exp(-q^2r^2/2)] - D). \tag{11}$$

Perturbations will grow when $Re(\lambda(q)) > 0$. We note that at $q = 0$, $Re(\lambda) = 0$. This implies that a homogeneous distribution is neutrally stable to homogeneous perturbations because of conservation of the total size of the population. We can investigate the sign of the above expression for $Re(\lambda)$ by looking for critical points of the expression

$$\phi(q) = (F[A_a a\exp(-q^2a^2/2) - A_r rF\exp(-q^2r^2/2)] - D). \tag{12}$$

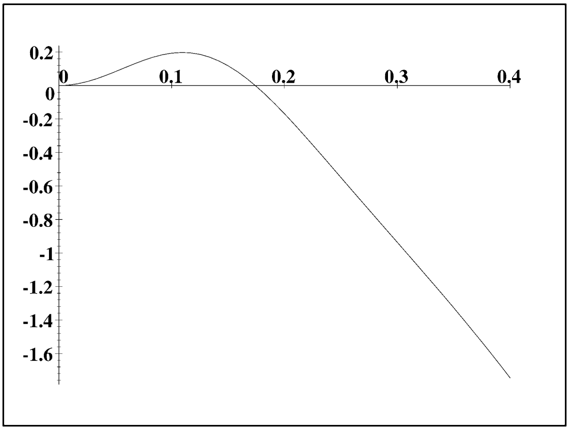
We find that $d\phi/dq = 0$ whenever $q = 0$ or

$$A_a a^3\exp(-q^2a^2/2) = A_r F r^3\exp(-q^2r^2/2). \tag{13}$$

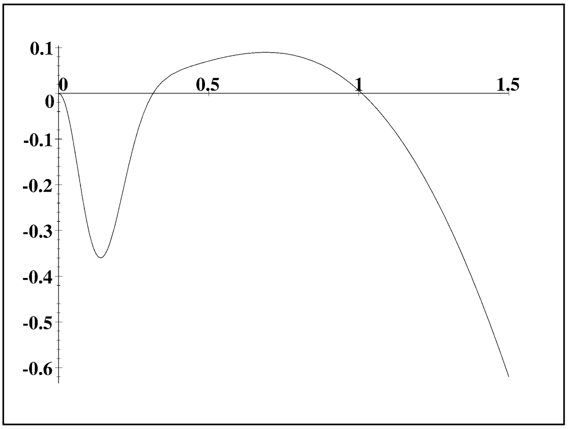
This latter condition is equivalent to

$$q^2 = 2\,\frac{(\ln(A_a a^3) - \ln(A_r F r^3))}{a^2 - r^2}. \tag{14}$$

This implies that a critical point of ϕ can occur at some finite real value of q in one of two possible cases: **Case (1)** $r < a$ and $A_r F < A_a$, which is biologically realistic. (In this case, these critical points are minima, and do not lead to growth, since λ is negative.) **Case (2)** $r > a$ and $A_r F > A_a$ which corresponds to a local maximum, and which results in positive λ and instability. A maximum of the linear growth rate in Case (2) corresponds to some finite wavenumber q, implying emergence of a periodic pattern (see Fig. 2). The fact that such periodicity is rarely if ever seen in swarms, stems from the fact that repulsion is usually much more localized than attraction in organism interactions.



Case (1)



Case (2)

Fig. 2. Plots of the growth rate λ (vertical axis) as a function of the wavenumber q (horizontal axis) for two values of the diffusion D. Parameter values used were: Case (1): $a = 10, r = 1, A_a = 5, A_r = 1, F = 1, D = 10$; Case (2): $a = 1, r = 10, A_a = 1, A_r = 5, F = 1, D = 0.6$.

(Note that the opposite balance of positive and negative effects occurs in chemical systems in which long-range inhibition and short-range activation gives rise to Turing-like instabilities.)

In the biologically realistic case, instability can occur only in a small range of values of wave numbers close to the origin provided that the diffusion coefficient, D, is small enough (see Fig. 2). This type of instability represents the onset of aggregation and formation of the swarm (Gross and Hohenberg, 1993).

In this case, considering small values of q leads to

$$\mathrm{Re}\,\lambda(q) \approx ((A_a a - A_r r F)\, F - D)\, q^2.$$

Let us analyze the simplest case $a = r$. Instability now depends on the sign of the expression:

$$s = -A_r F^2 + A_a F - D/r.$$

When s is positive, $\mathrm{Re}(\lambda) > 0$ implying instability and aggregation. Viewed as a function of F (the density of the homogeneous distribution), this equation describes a parabola opening down, so that positive s can occur only if the value of $s_{\max}$ at its vertex (which occurs at $F = A_a/2A_r$) is positive. From this observation we note the following: First, instability occurs only for some range of densities which are neither too low nor too high. Second, the *most unstable* density is one half the level at which attraction and repulsion just balance. Further, the condition that $s_{\max} > 0$ leads to the inequality

$$2\,\frac{D}{r} < \frac{A_a^2}{A_r}.$$

This inequality can be interpreted as a comparison of two speeds: the average speed of diffusion $(2D/r)$ through one interaction distance and the average attraction speed induced on an organism by a density A_a/A_r.

The instability corresponding to long wave-length perturbations occurs either if the diffusion is low, or if attraction is high. If repulsion or diffusion are strong and/or attraction is weak, then the organisms do not aggregate.

5. Swarm shape and propagation

In what follows, we consider a rectangular pulse ansatz solution of the equation

$$\frac{\partial f}{\partial t} = \frac{\partial}{\partial x}\left(D(f)\,\frac{\partial f}{\partial x}\right) - \frac{\partial}{\partial x}\left((a_e f + (A_a - A_r f)(K_o * f))\, f\right), \tag{15}$$

where the piecewise constant kernel:

$$K_o(x) = \begin{cases} -(1/2r)\,\mathrm{sign}(x), & -r \leqq x \leqq r \\ 0, & |x| > r, \end{cases} \tag{16}$$

will be used to compute approximate swarm shapes. For distances smaller than r, the interactions are constant. Beyond r, there are no interactions. Note that the density dependence is still distinct for the attraction and the repulsion, but that both have the same spatial range.

We investigate the stability of the ansatz solution, and perform an asymptotic analysis of the slowly decaying traveling wave. In the case of density-dependent diffusion, we will obtain a locally stable traveling band solution. After that, we look at certain perturbations including the effect of even nonlocal terms and more realistic kernels and speculate on the general case. Finally, we support these analyses with numerical studies.

In the limiting case in which the diffusion is absent, $D = 0$, we postulate that there exists a solution of equations (15) with kernel (16) of the form:

$$f(z) = FH_L(z), \tag{17}$$

where $z = (x - tV_{drift})$ is the traveling wave coordinate and $H_L(x)$ is a rectangular pulse:

$$H_L(x) = \begin{cases} 0, & x < 0 \\ 1, & 0 \leqq x \leqq L \\ 0, & x > L. \end{cases} \tag{18}$$

In order for this pulse to be a solution, its amplitude, F must be given by

$$F = \frac{A_a}{A_r}, \tag{19}$$

i.e. the density inside the swarm is such that the repulsion and attraction are equal. The speed of the pulse, V_{drift}, has to be

$$V_{drift} = a_e F = a_e \frac{A_a}{A_r}, \tag{20}$$

and the width of the swarm is $L = N/F$.

This solution corresponds to a swarm of constant density, F, with velocity V_{drift} to the right (arbitrarily picked here as the axis favored for motion – biologically, this would depend on environmental cues). The fact that our ansatz is a solution is shown in Appendix I.

In this solution, the density of the swarm is defined by a balance of attraction and repulsion: the greater the attraction (and/or the smaller the repulsion) the higher the density of the swarm, and the smaller its size for a given total number of organisms. This is observed biologically: increasing the total number of organisms in the group tends to increase the width of the swarm, but the density at the core is usually not affected strongly (Okubo, 1980; Parrish et al., 1997; Miller and Stephen, 1966).

6. Stability of the edges of the swarm

Consider the situation when density independent diffusion is very small, but non-zero. Then we use singular perturbation theory to investigate a nearly rectangular swarm profile. From now on, we will be working in a coordinate system moving with the swarm. This means that any individual motion is superimposed on a constant drift with magnitude (20). We use the moving coordinate z, introduced above (with $z = 0, z = L$ corresponding to the rear and front edges of the swarm, respectively). Then in this coordinate system, the density $f(z)$ of the swarm satisfies:

$$D\frac{d^2 f}{dz^2} - \frac{d}{dz}([a_e(f - F) + (A_a - A_r f)(K_o * f)]f) = 0. \qquad (21)$$

Integrating equation (21) once with respect to z leads to the first order ODE:

$$D\frac{df}{dz} - [a_e(f - F) + (A_a - A_r f)(K_o * f)]f = J, \qquad (22)$$

where the constant of integration J has the meaning of flux.

To nondimensionalize the model, consider the equilibrium density at the core of the swarm $F = A_a/A_r$ as the unit of density, the drift rate of the swarm $V_{drift} = a_e F$ as the unit of velocity, and the range of interaction r as the unit of length. Then the dimensionless equation for the density $f'(z')$, where $f = Ff'$ and $z = rz'$, has the form:

$$\varepsilon\frac{df'}{dz'} - [(f' - 1) + k(1 - f')(\tilde{K}_o * f')]f' = j. \qquad (23)$$

Here the dimensionless parameters

$$\varepsilon = \frac{D}{r(a_e F)}, \qquad k = \frac{A_a}{a_e}, \qquad j = \frac{J}{a_e F^2}$$

reflect the magnitudes of the diffusion, the strength of interaction and the flux, respectively. The dimensionless kernel is defined as $\tilde{K}_o(z') = rK_o(z/r)$.

We are interested in the limit of weak diffusion: $\varepsilon \ll 1$. We rescale the spatial variable: $y = z'/\varepsilon$ and assume that the function f' has the following asymptotic expansion:

$$f' = \sum_{n=0}^{\infty} \varepsilon^n f_n,$$

where the zeroth approximation f_0 is the nondimensionalized rectangular pulse given by (18): $f_0 = H_l(\varepsilon y)$ ($l = L/r$ is the nondimensionalized size of the swarm). We also assume (to be confirmed *a posteriori*) that the flux j is exponentially small with respect to ε, and, thus, that the right hand side of any equation for a finite order approximation would be equal to zero.

It is easy to check (see Appendix I) that the zeroth approximation, f_0, satisfies the equation obtained by collecting the terms of the zeroth order with respect to ε after plugging in the power series for f' into equation (23). We will now find the first approximation f_1 by collecting the corresponding terms of first order and solving the resulting equation:

$$\frac{df_1}{dy} - [(f_0 - 1) + k(1 - f_0)(\tilde{K}_o * f_0)] f_1 - [f_1 + k(1 - f_0)(\tilde{K}_o * f_1) - kf_1(\tilde{K}_o * f_0)] f_0 = 0. \tag{24}$$

On the interval $[0, l]$ the solution of equation (24) just gives a small correction to the constant density. Outside this interval, where $f_0 = 0$, the first approximation, though small, is of crucial importance since it carries information about the stability of the swarm. Because $f_0 = 0$ when $z' < 0$ or $z' > l$, equation (24) simplifies significantly to the following linear equation:

$$\frac{df_1(y)}{dy} - V(y) f_1(y) = 0, \qquad V(y) = -1 + k(\tilde{K}_o * f_0)(y). \tag{25}$$

The convolution in the above expression is easy to find, and the velocity is given by:

$$V(y) = \begin{cases} -1, & \varepsilon y \geqq (l + 1) \\ -1 - (k/2)(l - \varepsilon y + 1), & l < \varepsilon y < l + 1 \\ 0, & 0 \leqq \varepsilon y \leqq l \\ -1 + (k/2)(\varepsilon y + 1), & -1 < \varepsilon y < 0 \\ -1, & \varepsilon y \leqq -1. \end{cases} \tag{26}$$

This velocity profile is shown in Fig. 3. The fact that the velocity $V(y) = 0$ for $1 < \varepsilon y < l - 1$ can be seen from symmetry arguments. A less obvious statement, that this velocity is zero also at the edges of the swarm, (at $0 < \varepsilon y < 1$ and $l - 1 < \varepsilon y < l$) follows from a continuity argument, from the fact that the local drift term is constant everywhere inside the swarm where the density is constant, and from the choice of kernels. The change in the aggregation term near the edges is exactly counterbalanced by the change in the anti-crowding term for the right swarm density.

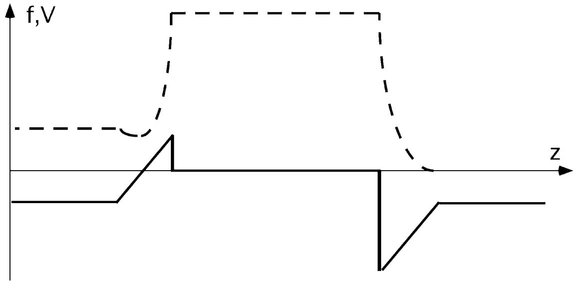


Fig. 3. Dashed line: the predicted shape of the propagating swarm. Solid line: the velocity profile of an individual organism induced by the rectangular swarm.

The swarm actually deviates from its idealized rectangular shape, but we will show that such deviations are relatively small when the diffusion is low. We now look more closely at each part of the swarm and compute the actual density distribution by solving the appropriate equation.

6.1. Density behind the swarm

The solution of equations (25) and (26) has the dimension-carrying form:

$$f(z) = C \exp\left[\frac{A_a^2 r}{4A_r D}\left(\frac{z}{r} + 1 - \frac{2a_e}{A_a}\right)^2\right], \quad -r < z < 0, \qquad (27)$$

where the constant C is found from the continuity condition at the rear edge of the swarm ($z = 0$):

$$C = \frac{A_a}{A_r} \exp\left[-\frac{A_a^2 r}{4A_r D}\left(1 - \frac{2a_e}{A_a}\right)^2\right]. \qquad (28)$$

For $z \leqq -r$, the velocity $V(z)$ is a negative constant in the coordinate system being used. (Organisms appear to move backwards relative to the coordinate system moving with the swarm.) Two possible solutions are a constant and an exponentially divergent one. Biologically, only the first of these is meaningful, and by continuity, this solution is:

$$f(z) = \text{constant} = \frac{A_a}{A_r} \exp\left[-\frac{A_a^2 r}{4A_r D}\left(1 - \frac{4a_e}{A_e}\right)\right], \quad z < -r. \qquad (29)$$

(Note that this is a *constant*, not an exponentially decaying function.) This finding implies that the swarm leaves a trail of stragglers behind it, i.e. that individuals are continually being lost from the group.

The constant solution at negative values of z cannot be normalized, and, rigorously speaking, is inconsistent with the assumption of the finite size of the population. The approximate solution described above would be valid only on a spatial scale comparable to the size of the swarm. Outside of this range (at negative values of z such that $z \leqq -\bar{L}$, where $\bar{L} \sim L$) the function $f(z)$ must decrease to satisfy the conservation constraint.

6.2. *Density in front of the swarm*

Using the velocity at the front of the swarm (for $L < z$), solving equations (25) and (26), and using continuity conditions, as before, we obtain the dimension-carrying form:

$$f(z) = \begin{cases} \dfrac{A_a}{A_r} \exp\left[-\dfrac{A_a^2}{4A_r D}\left(1 + \dfrac{2a_e}{A_a}\right)(z - L) + \dfrac{A_a^2}{4A_r D}\,(z - L)^2/r \right], \\ L < z < L + r \\ C_1 \exp\left[-\dfrac{A_a^2 r}{4A_r D}(z - L - r)\right], \\ z > L + r \end{cases} \tag{30}$$

where

$$C_1 = \frac{A_a}{A_r} \exp\left[-\frac{A_a^2 r}{4A_r D}\left(1 + \frac{4a_e}{A_a}\right)\right].$$

Equation (30) describes the distribution at $z > L$. In this region the solution is exponentially decaying. Thus, the front of the swarm is stable, and the shape of the front is that of an exponentially decaying leading edge. The shape of the propagating swarm is illustrated in Fig. 3.

6.3. *Stability: size and lifetime of the swarm*

The flux of individuals away from the swarm will be equal to the product of the density of lost individuals and their rate of drift away from the swarm. This flux is given by the expression

$$J = a_e \frac{A_a^2}{A_r^2} \exp\left[-\frac{A_a^2 r}{4A_r D}\left(1 - \frac{4a_e}{A_a}\right)\right]. \tag{31}$$

It is impossible to eliminate this continual loss of individuals, but we can consider the circumstances under which this loss is relatively low. This flux is exponentially small provided that

$$4a_e < A_a \quad \text{and} \quad D \ll \frac{A_a^2 r}{4A_r}\left(1 - \frac{4a_e}{A_e}\right). \tag{32}$$

When this condition is satisfied, the loss will be minor on the time scale of observation.

We might ask what happens to the swarm as it shrinks due to loss of members. We see from this particular example that the core density, F, should not change, as it is prescribed by the density dependence of the velocity terms. However, to compensate for loss, the width of the swarm will decrease linearly. Using conservation of the total number of organisms, we find that the size of the swarm satisfies:

$$\frac{dL}{dt} = \frac{J}{F} = \frac{a_e A_a}{A_r} \exp\left[-\frac{A_a^2 r}{4A_r D}\left(1 - \frac{4a_e}{A_a}\right)\right]. \tag{33}$$

Thus, the width of the swarm will decrease exponentially slowly if conditions (32) are satisfied. The swarm will disappear after an exponentially large time $T \sim L/(dL/dt)$. The "lifetime" of the swarm is thus:

$$T \sim \frac{LA_r}{a_e A_a} \exp\left[\frac{A_a^2 r}{4A_r D}\left(1 - \frac{4a_e}{A_a}\right)\right]. \tag{34}$$

6.4. Density dependent diffusion

We consider density dependent diffusion whose magnitude decreases to zero as the local population density vanishes. We show that this type of density dependence can make the swarm locally stable.

We investigate the asymptotically small density at the rear edge of the swarm. (It was shown above that the front edge of the swarm is locally stable. A density dependent diffusion does not change this stability.) The simplest case to be considered is that of a linear density dependence. We deal with this case in detail. It is our belief that more complex density dependence which decreases to zero at least linearly (or faster) will lead to similar behavior.

Equation (25) with $V(y)$ given by (26) and density dependent diffusivity, Df, governs the asymptotically small density and can be rewritten in the form:

$$f_1(y)\,\frac{df_1(y)}{dy} - V(y)\,f_1(y) = 0. \tag{35}$$

Solving the equation

$$\frac{df_1(y)}{dy} - V(y) = 0,$$

and using the continuity boundary condition at the rear edge of the swarm we find the dimension-carrying form of the density distribution:

$$f(z) = \frac{A_a^2 r}{4A_r D}\left(\frac{z}{r} + c\right)^2 + h, \quad -r < z < 0, \qquad h = \left[\frac{A_a}{A_r} - \frac{A_a^2 r}{4A_r D}c^2\right]. \tag{36}$$

The equation for $f(z)$ then describes a parabola whose height above the z axis is given by h. For the following weak solution to hold, we require that this height be negative. This leads to the condition

$$D < \frac{A_a r}{4}\left(1 - \frac{2a_e}{A_a}\right)^2. \tag{37}$$

If this condition is valid then the weak solution of equation (35) is

$$f(y) = \begin{cases} \dfrac{A_a^2 r}{4A_r D}\left(\dfrac{z}{r} + c\right)^2 + \left[\dfrac{A_a}{A_r} - \dfrac{A_a^2 r}{4A_r D}c^2\right], & r(d-c) < z < 0 \\ 0, & z < r(d-c), \end{cases} \tag{38}$$

where

$$d = \sqrt{c^2 - \frac{4D}{A_a r}}, \qquad c = 1 - \frac{2a_e}{A_a}.$$

In this case, the density of the 'lost' organisms behind the swarm is zero, and the swarm is locally stable. We get a **true traveling band solution**. Otherwise, if the diffusion coefficient is too big, the inequality (37) is not satisfied, so that the density everywhere behind the swarm is non-zero and the local instability persists. The formal derivations here do not prove the uniqueness or stability of the traveling band solution, but this result will be supported with numerical studies below. It is hard to imagine that this scenario is realistic in the case of small organisms such as flying insects or small marine animals, since these are always subject to the random effects of turbulence that would impose a non-zero diffusion on any deterministic behavior. In the case of larger animals, such as, say, wildebeest, it is more realistic to believe that stragglers in the rear of the herd may stop meandering and random searching in favor of catching up with the rest of the herd.

6.5. Conclusions from analytical studies

The results of the findings in the above sections lead to the following conclusions:

1. **No global stability:** Even with non-local attraction, there does not appear to be a way to make the swarm globally stable. Diffusion, which formally has an infinite range, will move organism by distances greater than the range of interaction behind the swarm. Thereafter, they will no longer "sense" the swarm, according to our model. Then, the fact that the swarm is moving away (the stragglers have a negative drift relative to the swarm) will mean that they do not catch up. This conclusion follows from the qualitative assumption that denser patches move faster. If we assume the opposite, (i.e. that denser patches move more slowly) then the rear of the swarm is stable. However, it can be shown that under such circumstances, the front of the swarm becomes unstable.
2. **Dispersal for a rapidly moving swarm:** If $4a_e > A_a$, which means that advection is stronger than aggregation in some sense, then equation (29) implies that the density of the stragglers behind the swarm is greater than the density in the core. This contradicts our assumption and indicates that, in this case, the swarm is unstable to loss of individuals from the back and will deteriorate in finite time. (This will be demonstrated by numerical simulations.)
3. **Dispersal for large density-independent diffusion:** If diffusion is "fast enough", i.e. the value of D is comparable to or greater than $A_a(A_a - 4a_e)\,r/4A_r$, then the density of stragglers behind the swarm will not be small, and the swarm will also disperse in finite time.
4. **Exponential tail for low density independent diffusion:** If $D \ll A_a (A_a - 4a_e)\,r/4A_r$, the swarm leaves behind an exponentially thin layer of lost organisms given by equation (29).
5. **Local stability of the swarm for density dependent diffusion:** If the coefficient D in the diffusivity, Df, is small enough, i.e. $D < (A_a r/4)(1 - (2a_e/A_a))^2$, then the swarm is locally stable.

Although by remark (1) above, we have pointed to the global instability of this swarm, we also noted that the swarm can be quasi-stable, changing at an exponentially slow rate. By remarks in the introduction, as far as realistic biological predictions (rather than abstract mathematical solutions), this would be adequate to guarantee cohesiveness of the swarm on the time scale of observation. This analytical prediction is confirmed numerically below.

7. Numerical simulations

The analytical results of the previous sections were supplemented and verified with numerical studies. We approximated the original problem, which was posed on an infinite domain, with a model on a finite interval with periodic boundary conditions (the size of the domain is taken to be several times larger than the width of the swarm which is, in itself, a few times larger than the range of interactions). The domain was discretized by 100 grid points. Equations (15,16) were solved using a second order Lax–Wendroff algorithm (Nakamura, 1991). A time increment of $dt = 10^{-6}$ was used. The convolutions were approximated using a second order accurate trapezoidal rule. Tests of this numerical scheme for parameter values listed, and for various grid sizes, demonstrated that the numerical solutions gave good qualitative fit to the known approximate solutions of the original model.

In all simulations, the initial conditions were

$$f(x, t = 0) = 10H_{20}(x - 10),$$

i.e., a rectangular pulse of width $L = 20$ and density $F = 10$. The values of the attraction and repulsion parameters were $A_a = 20$, $A_r = 2$, respectively. With this choice of parameters and initial conditions, and with equal ranges of the attraction and repulsion, the initial density in the core of the swarm, $F = 10$, is equal to the equilibrium density $F = A_a/A_r$. This choice saves computation time, skipping transients that would occur while the equilibrium density of the swarm core was being established. (We checked separately that other initial conditions evolved into the equilibrium core density.) In the course of the simulations, the following governing parameters were changed: D, the diffusion coefficient, a_e, the amplitude of the even local density dependent drift term, A_e, the amplitude of the even non-local density dependent drift term, r_a, the range of attraction, and r_r, the range of repulsion.

8. Results of the numerical experiments

In order to observe the evolution of a propagating pulse, the results of the numerical experiments were plotted three times. The initial density profile (solid line), the profile after 1000 (dashed), after 2000 (dot dashed), and after 3000 time steps (dotted) are shown in the figures.

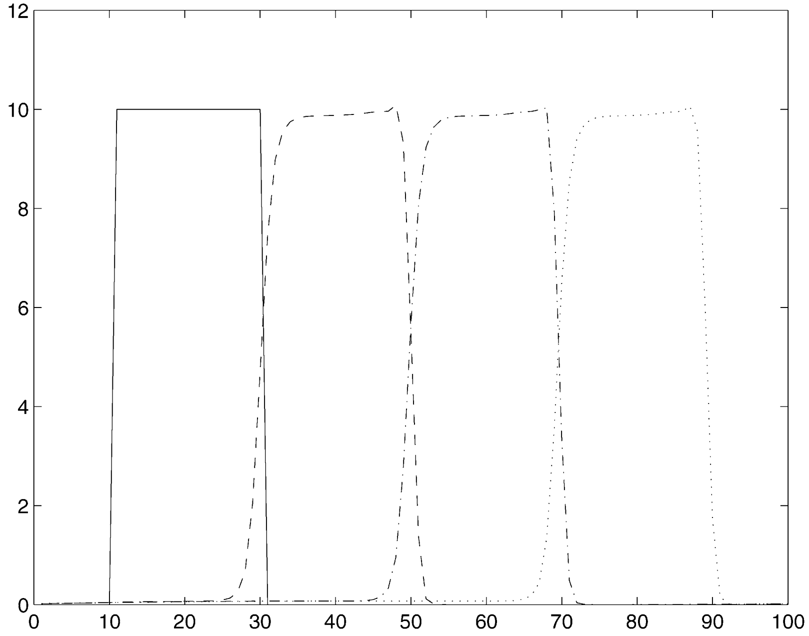


Fig. 4. Basic simulation with $A_e = 0, r_a = r_r = 5, a_e = 20, D = 5$.

8.1. Basic run; $A_e = 0, r_a = r_r = 5, a_e = 20, D = 5$

Figure 4 shows what happens in the **absence** of the even non-local density-dependent drift term ($A_e = 0$) and **equal** ranges of attraction and repulsion ($r_a = r_r = 5$). A nearly rectangular-looking pulse propagates virtually unchanged. A very thin layer of lost organisms can barely be seen behind the propagating swarm. The density at the front of the pulse decreases more rapidly than at the rear, while small increase in the density at the very front of the swarm, and the depletion at the very back of it can be seen. The following heuristic explanation is helpful.

Let us assume that a small, highly localized increase in density occurs somewhere in the core of the swarm. Then the velocity at the location of this perturbation will be greater than at other places in the core. This stems from the local density-dependent advection term and from the fact that non-local terms average to zero in the core. This means that such a perturbation would gradually drift to the front of the swarm. At the very front, this denser area will be preserved by attractive interactions. By a similar argument, a small, localized decrease in density would drift to the rear edge of the swarm. This suggests that there should be a denser area at the front edge of the swarm, and a sparser area at its rear edge.

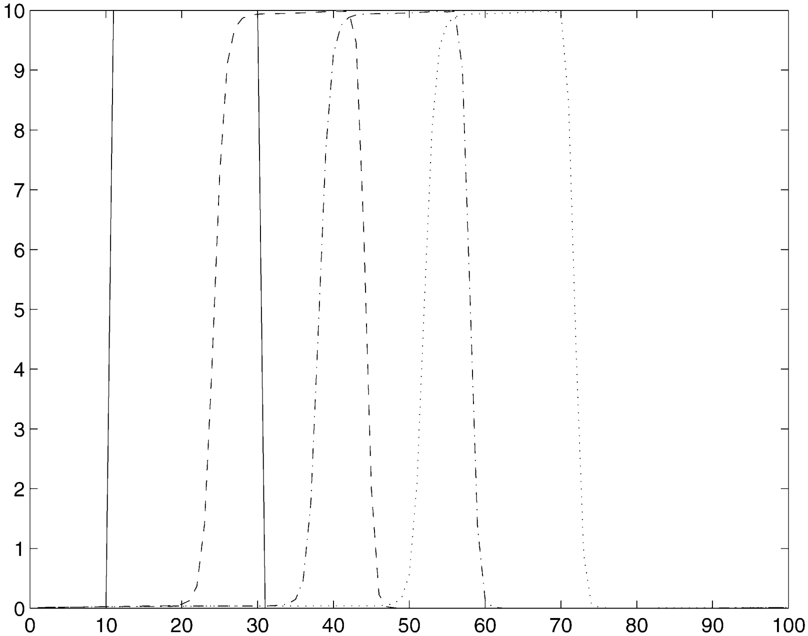


Fig. 5. Results of a simulation with small, even, non-local, drift term.

8.2. Effect of non-local even drift term

As shown in Fig. 5, we next introduced a small, even, non-local, density dependent drift term:

$$V(f) = a_e f + (A_a - A_r f)\,(K_o {*} f) + A_e(K_e {*} f), \qquad A_e = 2 \ll A_a, \quad (39)$$

where only the last term, considered as a perturbation, is new, and where the **non-local drift kernel**, K_e is defined on the interval $[-r_e, r_e]$, $r_e = 1$ as follows:

$$K_e(x) = \begin{cases} \dfrac{1}{2r_e}, & -r_e \leqq x \leqq r_e \\ 0, & |x| > r_e. \end{cases} \quad (40)$$

All other parameters had their previous values.

As seen from Fig. 5, this kind of perturbation makes the shape of the propagating swarm more perfectly rectangular. Qualitative arguments about this effect are as follows. As a first approximation, the change in the velocity due to this perturbation will be constant and small in the core of the swarm (at $r_e < z < L - r_e$). At the front ($0 < z < r_e$) and rear ($L - r_e < z < L$) edges of the swarm, the effect of the perturbation convolution term decreases because the number of

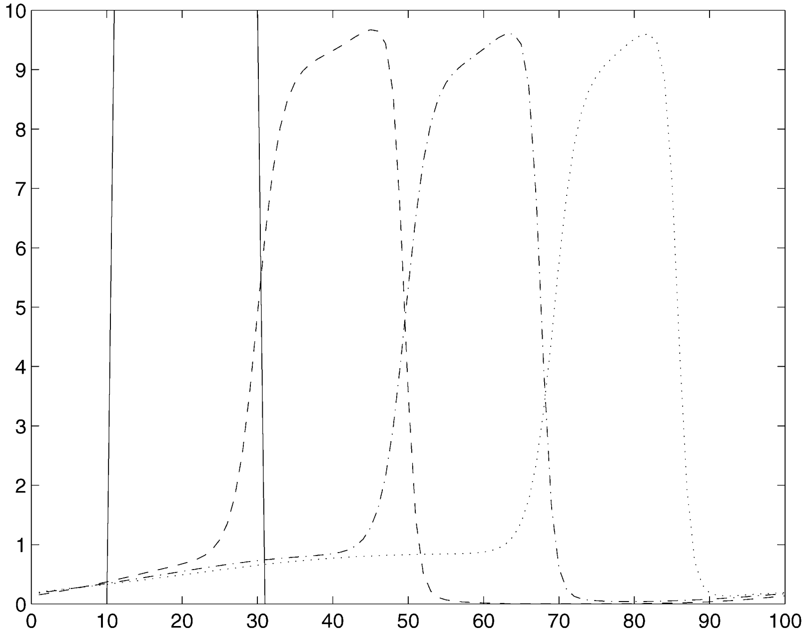


Fig. 6. Effect of diffusion: $A_e = 0, r_a = r_r = 5, a_e = 20, D = 8$.

organisms inside the interaction range gets smaller. This means that there is a decrease in the velocity at the edges (relative to the velocity at the center of the swarm). The consequence of this decrease will be a small flux of organisms from the core to the rear edge, and from the front to the core. This flux smoothes out the denser front and the sparser rear, leading the shape of the swarm to become a more perfect "rectangle".

8.3. Effect of diffusion

In Fig. 6, we used the original parameters, but increased the diffusion coefficient to $D = 8$. In agreement with the theoretical predictions, the density of the stragglers grows significantly as the dispersal intensifies. This density gradually becomes homogeneous behind the propagating pulse. Furthermore, the front of the pulse is now visibly denser than its rear. The graph also confirms the conclusion that the height of the pulse (core density) hardly changes, while the width of the pulse decreases due to loss of organisms.

For Fig. 7, diffusion was increased further to the value $D = 11$. Now, this strong dispersal destroys the swarm in finite time: the density of the individuals shed from the rear of the swarm is comparable to the

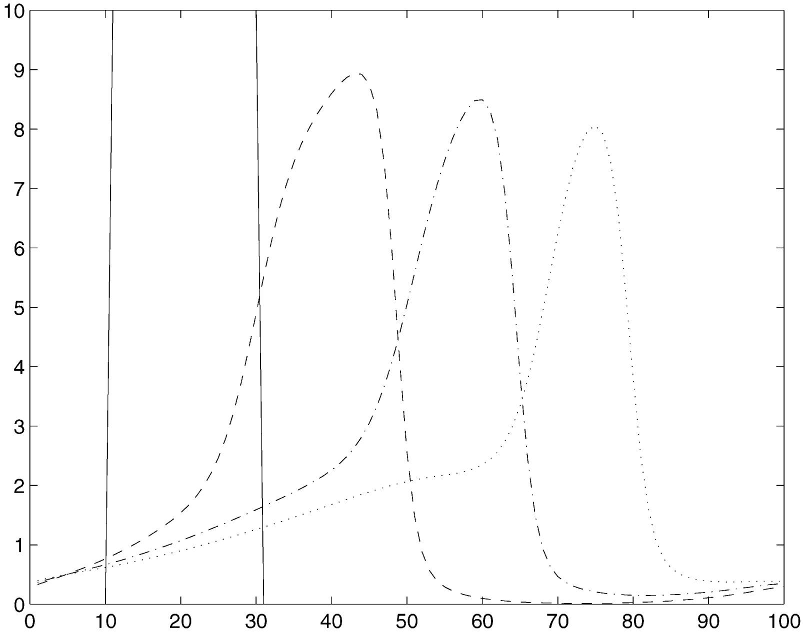


Fig. 7. Effect of diffusion: as in Fig. 6 but with $D = 11$.

density of the swarm, and both height and width of the pulse decrease rapidly.

8.4. Effect of density-dependent diffusion

We consider a combination of the diffusion behavior as follows: for moderate densities, $f > 0.1F$, we use a density independent diffusion with a constant diffusion coefficient, D. (This was done to avoid excessive growth of the diffusion at high densities.) At small densities, $f < 0.1F$, we used the density dependent diffusion, Df. The results are presented in Fig. 8. Here we show the swarm profile after 3000 steps corresponding to the model parameters $A_e = 0$, $r_a = r_r = 15$, $a_e = 20$, $A_a = 20/3$, $A_r = 2/3$, $D = 12$. The density profiles in both cases are roughly the same. However, the fine structure of the densities at the rear of the swarm exhibit an important difference. The figure inset (shown magnified below) reveals that in the density independent case (solid curve), a small constant density of ‘lost’ organisms is left behind the swarm. This would lead to the eventual disintegration of the swarm. In the density dependent case (dashed curve), the density of organisms behind the swarm falls sharply to zero (to a level of accuracy greater than the error in the numerical method).

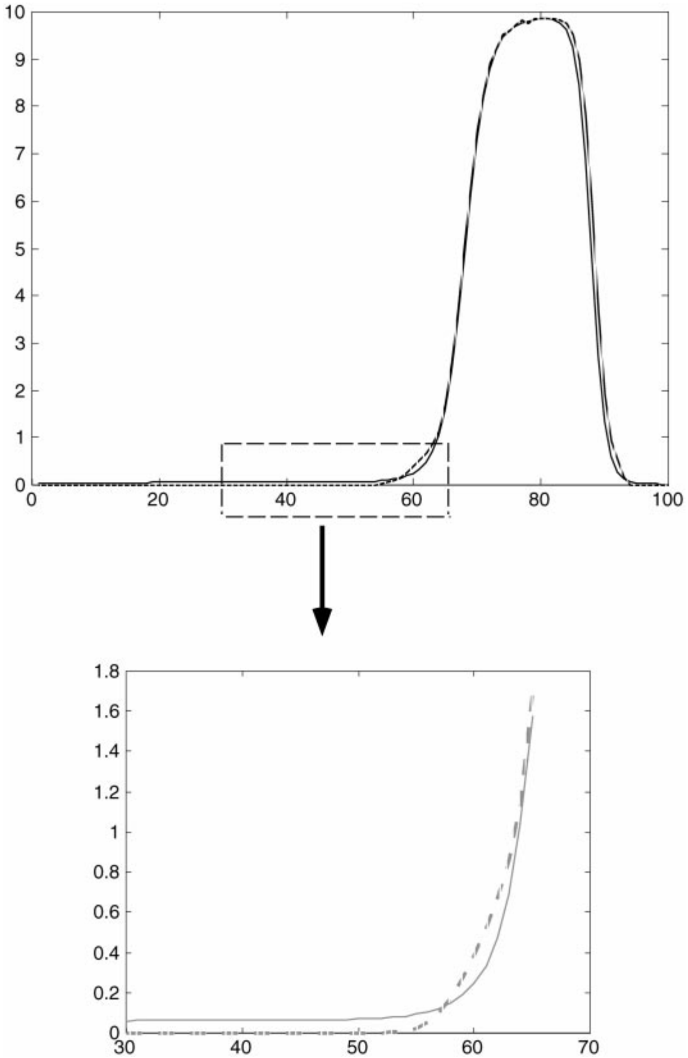


Fig. 8. Comparison of the cases of density independent (solid curve) and density dependent diffusion (dashed curve). The parameters were $A_e = 0$, $r_a = r_r = 15$, $a_e = 20$, $A_a = 20/3$, $A_r = 2/3$, $D = 12$.

8.5. Effect of range of attraction

In Fig. 9, the original parameters were used but with the range of attraction increased to $r_a = 6$. Effectively, this results in stronger attraction, and we see that loss of organisms is imperceptible. The swarm is maintained as a unit, its average density increases, and it then accelerates in comparison with the unperturbed case. Due to a more

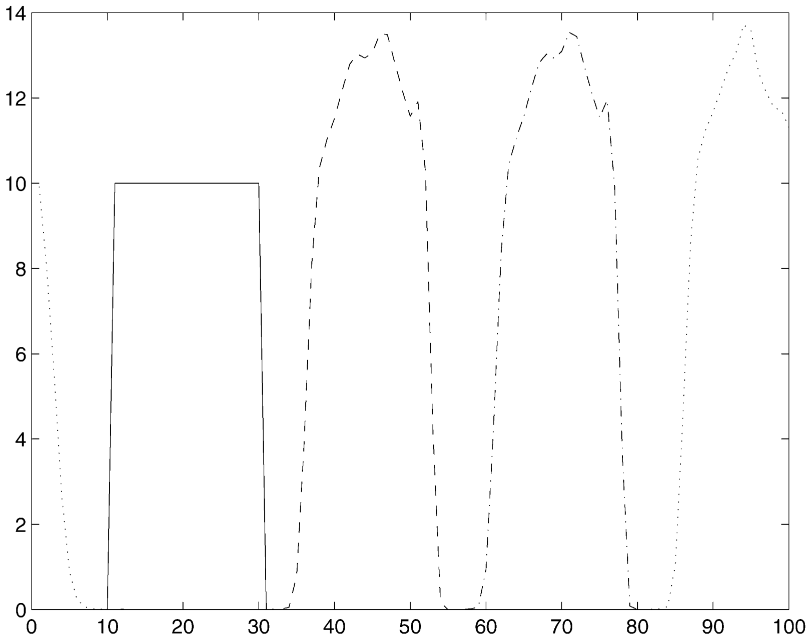


Fig. 9. Effect of increasing the range of attraction: Results of a simulation with $A_e = 0, r_a = 6, r_r = 5, a_e = 20, D = 5$.

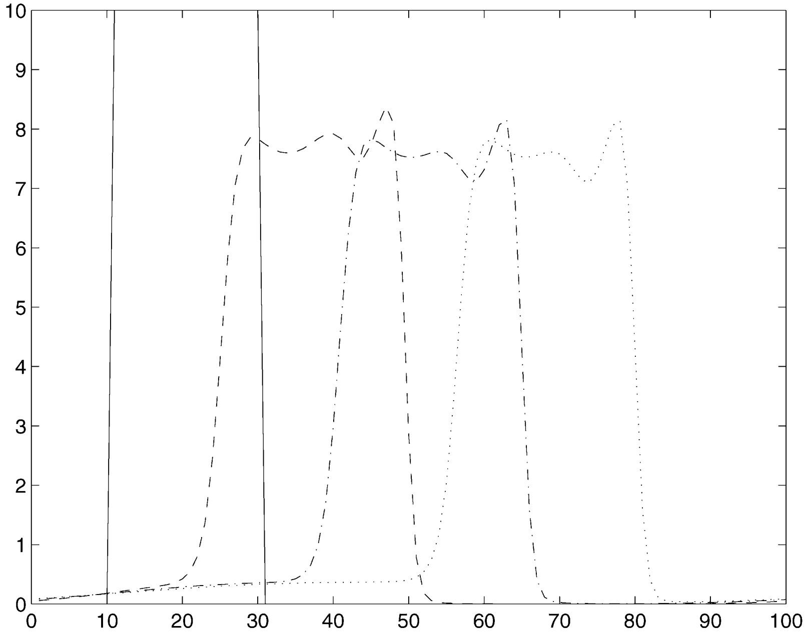


Fig. 10. Effect of decreasing the range of attraction: Results of a simulation with $A_e = 0, r_a = 4, r_r = 5, a_e = 20, D = 5$.

complex balance between attractive and repulsive interactions, some more irregular and evolving profile is observed in the swarm.

For the simulation shown in Fig. 10, the range of attraction was decreased to $r_a = 4$. Due to effectively weaker attraction, loss of organisms in this case is noticeable, significantly greater than in the first, unperturbed, case. The average density of the pulse decreases, and the swarm moves more slowly in comparison with the unperturbed case. The complex balance between attractive and repulsive interactions leads to a more irregular, oscillatory profile which evolves with time. Spatial oscillations are predicted from the linear stability analysis in this case, since the repulsion is larger than the attraction.

8.6. Effect of an even local drift term

In Fig. 11, the ranges of attraction and repulsion were set equal, and the even non-local term was absent. The even local term was increased 2.5 times to $a_e = 50$ in order to investigate the predicted instability. In order to better observe the evolution of the swarm, the results were plotted after 1500 (dashed), and 3000 (dotdashed) time steps. Because

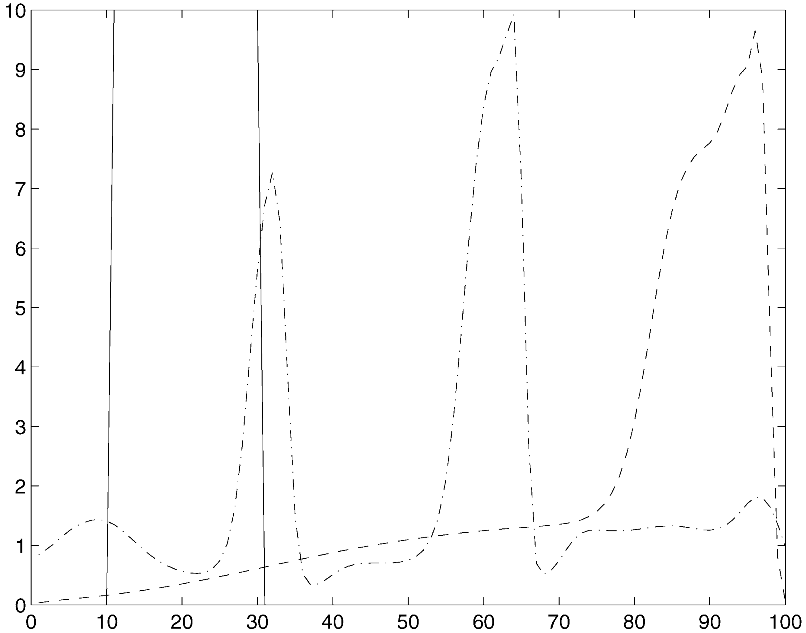


Fig. 11. Effect of increasing the even local drift term: Results of a simulation with $A_e = 0, r_a = r_r = 5, a_e = 50, D = 5$.

of the greater times of simulation and speed of motion, the swarm revolved around the periodic domain several times. In agreement with the analysis, the stability of the swarm was broken: the density of lost individuals increased significantly in comparison with the first case, and the shape of the swarm changed. Of great interest is the fact that the regime of swarm dispersal differs here from the smooth dispersal observed in previous cases. Indeed, a second, smaller, peak appears behind the "main" swarm after 3000 time steps. After that, (not shown) two narrow peaks propagate for a long time without changing their shape, with the smaller peak moving more slowly than the larger one.

This result can be understood as follows: Initially, an increase in the even, local, density dependent drift causes the stragglers in the wake of the swarm to lose speed relative to the swarm. This results in a greater flux from the rear of the pulse and more stragglers. As these stragglers get more numerous, attractive interactions among them start to dominate, and a new aggregation starts to form behind the main swarm. As this new group is less dense than the original swarm, it moves more slowly, and eventually has a diminishing effect on the core of the original swarm. The even drift is not as destructive any more, and both the new group and the main swarm (now smaller and less susceptible to drift-induced instabilities) coexist, and stabilize. The original group splits into two groups, traveling with different speeds. If the swarm is initially large, it may split into more than two groups. However, even these groups are not globally stable, and will slowly disperse.

8.7. Results for Gaussian kernels

In the final test, shown in Fig. 12, we used a more generic Gaussian form of the integral kernels:

$$K_e(x) = \exp(-x^2/r_e^2), \qquad K_o(x) = -\, x \exp(-x^2/r^2). \tag{41}$$

Here r_e is the scale of the range of the even drift term, and r is that of the odd terms. The odd kernel was used by Kawasaki (1978) in a model for spatial distribution of organisms. The values of the parameters we used for this simulation were: $D = 5$, $a_e = 0$, $A_e = 1$, $A_a = 20$, $A_r = 2$, $r_e = r = 5$. The swarm propagates with roughly constant shape. As before, when the amplitude of the even term A_e is large enough, the swarm becomes unstable. Making the ranges of attraction, repulsion and the even term different, and changing the form of the kernel causes changes in the shape of the swarm, but does not lead to its destabilization if the attraction is sufficiently great and the even drift is sufficiently weak (not shown). This illustrates that the symmetry, rather

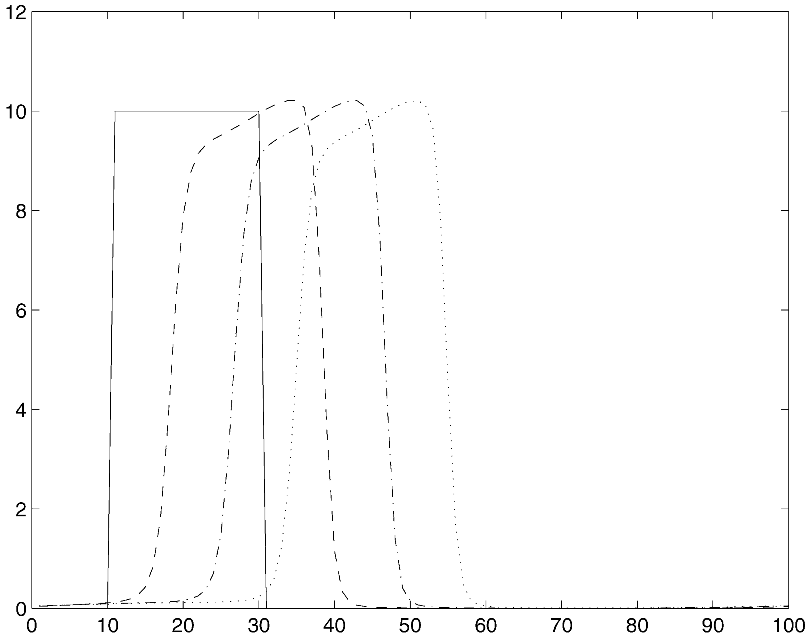


Fig. 12. Effect of Gaussian kernels (see text). Results of a simulation with $D = 5$, $a_e = 0$, $A_e = 1$, $A_a = 20$, $A_r = 2$, $r_e = r = 5$.

than the detailed form of the integral kernels is important for the qualitative results of this paper, confirming previous experience with non-local models (Mogilner and Edelstein-Keshet, 1996).

9. Conclusions and discussion

Our main result in this paper is that the propagating swarm of organisms, though not globally stable, can be long lasting. The effect that leads to a long-lived swarm is mutual non-local attraction of individuals. Repulsion limits the swarm density and prevents collapse of the swarm. We have also shown that in the case of density dependent diffusion, true locally stable traveling bands can occur.

The assumptions that were made in building the model may seem overly restrictive at first. However, the simplifications have allowed a rather complex set of interactions to be thoroughly explored analytically and numerical results can be understood much more fully. Some variations of the strict simplifications were explored numerically. We have seen that the detailed shapes of the kernels that describe non-local effects are not very important, but that their symmetry properties have a large impact.

We have concentrated, here, on investigating the case of non-local advection, leaving the dispersal term in a more traditional local form. Convection terms lead to attraction, repulsion, aggregation and macroscopic motion. Dispersal is a disordering and a smoothing influence. The effects of generalized diffusion have been explored to some extent (Cohen and Murray, 1981; Murray, 1989). It appears that, mathematically, diffusion with non-local effects does not lead to qualitatively new patterns (Turchin, 1986).

Is it really necessary to include non-local effects to get a semi-realistic swarm behavior? Can similar quasi-stable swarms be obtained with strictly local terms, as in the traditional PDE's? As mentioned in the introduction, non-local effects can be neglected when the population density changes slowly on a spatial scale comparable to the interaction range. When this is not the case, for instance at the sharp edges of the swarm, any local approximation becomes inadequate (Grunbaum and Okubo, 1994). If we were to approximate our integro-differential model with a non-linear PDE, then the traveling wave solution would not be found, even if higher derivative terms are kept. It turns out that the short wave-length phenomena at the edges of the swarm are vital.

It is shown in Appendix II, that the dispersion relation for the analogous higher derivative model (obtained by a Taylor expansion of the convolution terms) has the form:

$$\lambda = -Dq^2 + F[-ia_e q + (A_a - A_r F)(aq^2 - bq^4 + \cdots)],$$

where $a \gg b > 0$. We recognize that the term aq^2 corresponds to a negative diffusion which would lead to an ill-posed problem as discussed in Alt (1985). The problem is due to the fact that modes with increasing q are more and more unstable. (This corresponds to unbounded instabilities on an arbitrarily short length scale.) It would appear that the term $-bq^4$ can eliminate this difficulty, but we observe that the coefficient, $(A_a - A_r F)$ can be either positive or negative, depending on the size of F relative to A_a/A_r. But this value is the level of the equilibrium density inside the swarm, so that small perturbations can make the sign of the term $(A_a - A_r F)$ fluctuate. This means that the fourth order term will actually lead to even worse instabilities. A similar conclusion applies for any number of terms in such local approximations.

In previous literature, (Murray, 1989; Cohen and Murray, 1981; Ochoa, 1984), local approximations corresponding to the above two terms in our expansion were used to model so-called generalized diffusion. In these models, absence of wild instabilities was due to the absence of repulsion (i.e. $A_r = 0$). However, as we have argued, this term is essential if it is desired to reproduce a swarm whose internal density is constant (not a goal of the above papers).

Our main result is still that an exact traveling band solution only exists under restrictive assumptions, and that more generally, a band-like solution can be stable only for some limited (if possibly long) lifetime. This leaves us wondering why it appears that flocks of birds stay together, and that individuals are not lost in the most commonly recognized animal aggregations. We might speculate that first, the time of observation may be short compared with the exponential time scale on which significant loss occurs (the solution decays on greater time scale). Second, the continuous description of the swarm may be inadequate in the case of a limited number of organisms. These speculations, which were already voiced in a previous paper (Edelstein-Keshet et al., 1997) may partly explain the disparity between the idealized model pulses and the true behavior of swarms.

Acknowledgements. We thank James Watmough and the anonymous reviewers for valuable suggestions. LEK is supported by an NSERC (Canada) operating grant (GSC21). AM is currently supported by NSF grant (DMS 9707750).

Appendix I: Verification that the rectangular ansatz is a solution

We consider the case that $D = 0$ and show that the rectangular pulse, given by (17), is a solution of the model consisting of equations (15,16).

For $r < x < L - r$ the last two integral terms in equation (15) cancel by symmetry of the kernels. Then, if at such $x, f = F =$ const, we have

$$\frac{\partial f}{\partial t} = -(a_e F)\frac{\partial f}{\partial x},$$

which allows the solution (17) where, so far, we have $V_{drift} = a_e F$ defined, but F is still to be found. At $0 < x < r$ the repulsion term in (5) contributes the value $-A_r F^2(r - x)/2$ to the drift velocity, while the aggregation term contributes the value $+A_a F(r - x)/2$. The contribution of the drift term is $a_e F$. To ensure the existence of the ansatz solution,

$$V(x) = a_e F + A_a F(r - x)/2 - A_r F^2(r - x)/2 = V_{drift} = a_e F$$

independently of x, so

$$A_a F = A_r F^2.$$

Thus we find the density of the swarm $F = A_a/A_r$ from these boundary conditions. The same is true for $L - r < x < L$:

$$V(x) = a_e F + A_a F(x - L + r)/2 - A_r F^2(x - L + r)/2 = V_{drift} = a_e F$$

and again $F = A_a/A_r$. For $x < 0, x > L$ the statement is obvious.

Appendix II: Local approximation

We reason here that there is no sensible local approximation to our non-local model. Let us assume that the range of interaction is very small, and that the density $f(x, t)$ changes on a longer spatial scale. In this case, we can use a Taylor approximation:

$$f(x') = f(x) + (x' - x)\frac{\partial f(x)}{\partial x} + \frac{(x' - x)^2}{2}\frac{\partial^2 f(x)}{\partial x^2} + \frac{(x' - x)^3}{6}\frac{\partial^3 f(x)}{\partial x^3} + \cdots.$$

Then,

$$(K_o * f)(x) = a\,\frac{\partial f(x)}{\partial x} + b\,\frac{\partial^3 f(x)}{\partial x^3} + \cdots, a \gg b,\ a = -\int_{-\infty}^{\infty} xK_o(x)\,dx,$$

$$b = -\int_{-\infty}^{\infty} x^3 K_o(x)\,dx.$$

Then our model assumes the local form:

$$\frac{\partial f}{\partial t} = D\frac{\partial^2 f}{\partial x^2} - \frac{\partial}{\partial x}\left[a_e f^2 + af\frac{\partial f}{\partial x}(A_a - A_r f) + bf\frac{\partial^3 f}{\partial x^3}(A_a - A_r f) + \cdots\right].$$

Linear stability analysis shows that if we let $f(x, t) = F + ce^{\lambda t}e^{iqx}$, we would obtain the dispersal relation:

$$\lambda = -Dq^2 + F[-ia_e q + (A_a - A_r F)(aq^2 - bq^4 + \cdots)].$$

As discussed in Section 9, this expression indicates that a purely local model would have deficiencies that cannot be easily overcome.

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